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The population ecology of soil testate rhizopods on the sub-Antarctic island of South Georgia

BY

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INTRODUCTION

Testate rhizopods occur in many types of terrestrial habitats, but are particularly abundant in soils and peats with a high organic content such as occur in forests, moorland and polar tundra. Studies on the population ecology of testate rhizopod species (SMITH, 1973 b; LOUSIER, 1974; COUTEAUX, 1975, 1976; LAMINGER, 1978; BONNET, 1981) emphasised that available moisture was an important factor influencing the size and activity of populations. Other significant influences included temperature, soil pore dimentions, availability of minerals for test construction and nutritional factors. In Antarctic and high altitude regions, where the soil is frozen for several months every year (SMITH, 1973 b; LOUSIER, 1974; LAMINGER, 1978), the testate populations showed cessation of activity during the winter and population blooms associated with the spring melt. During this period, relative growth rates of the populations of up to 5.0 % individuals day^{-1} were commonly observed and up to 10.0 % day^{-1} on occasion. Similar spring blooms of populations have also been observed in temperate forest soils (COÛTEAUX, 1976).

The occurrence of testate rhizopods on the sub-Antarctic island of South Georgia (54-55° S; 36-38° W) (Fig. 1) has been reported by RICHTERS (1908), SANDON and CUTLER (1924) and SMITH (1978, 1982 b). A total of 29 species has been recorded from a variety of habitats, but there are no previous quantitative observations on the testate populations. The purpose of the present study was to determine the sizes and seasonal fluctuations in the populations

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of testate rhizopods in four contrasting habitats on South Georgia, to relate the results to available data on the physical and biotic environment, and to compare the results with those of previous studies in Antarctic, sub-Antarctic and Alpine regions.

I. — FIELD SITES

The study was carried out in the Cumberland East Bay area on the north-east coast of South Georgia (Fig. 1). Located here are the largest areas of ice-free ground on South Georgia and also the most mature soils and plant communities on the island (SMITH and WALTON, 1975). The four sites selected for regular sampling (Fig. 2), each represented a different vegetation, and hence habitat, type. Biological and environmental studies have been undertaken at these sites since 1976.

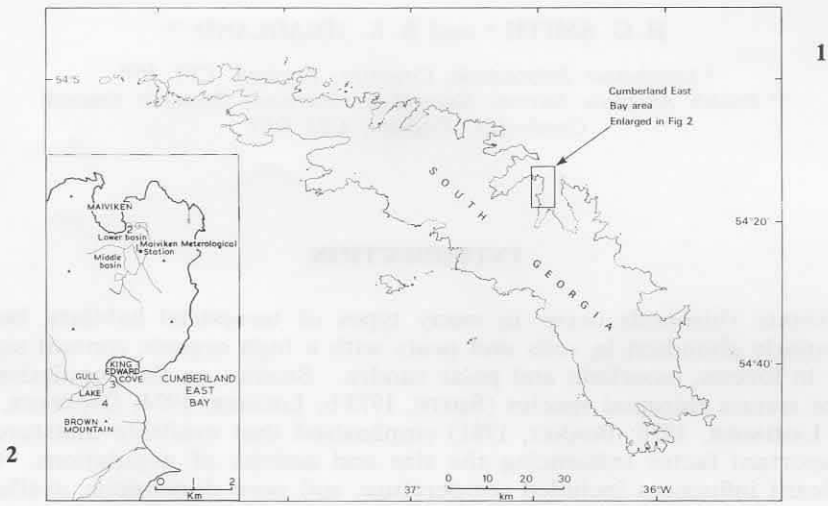


FIG. 1. — Map of the island of South Georgia showing the location of the study area. FIG. 2. — Map of the Cumberland East Bay area of South Georgia showing the location of the study sites: 1. *Festuca*, 2. *Polytrichum*, 3. *Acaena*, 4. *Tortula-Rostkovia*.

SITE 1 is a relatively dry grassland dominated by the short erect tufted fescue *Festuca contracta* with moss *Chorisodontium aciphyllum* and lichens *Cladonia* spp. as the chief associates. It occupies the southwest-facing slope of a ridge north east of the large lake in Maiviken middle basin, at 80 m altitude. The soil consists of a 2 cm organic layer of litter and humus (pH 3.9) overlying a brown loam-like soil with small stones (pH 4.2).

SITE 2 is an ombrogenous raised bog dominated by the tall turf-forming moss *Polytrichum alpestre* with *Chorisodontium aciphyllum* and the rush *Juncus scheuchzerioides*. It lies at 15 m altitude in a sheltered rock basin among knob and tarn topography in Maiviken lower basin. Accumulation of peat (pH 4.2) below the moss reaches 200 cm depth. This type of moss-turf formation is typical of the maritime Antarctic zone, and

closely resembles Signy Island terrestrial reference site 1 in the South Orkney Islands (TILBROOK, 1973) where population studies on testate rhizopods have been made previously (SMITH, 1973 a, 1973 b).

SITE 3 is a herbfield, occupied by a closed community of the deciduous shrublike *Acaena magellanica*, situated on a north-facing slope east of Gull Lake stream between 5 and 15 m altitude. Owing to its sheltered northerly aspect and low altitude, this site is often snow-free from earlier in the spring each year than the other sites. A distinct layer of *Acaena* leaf litter about 5 cm thick (pH 4.6) has accumulated below the canopy and this overlies an organic loam soil (pH 3.8).

SITE 4 is a wet, seepage slope mire dominated by the moss *Tortula robusta* with scattered plants of the rush *Rostkovia magellanica*. The slope dips gently westwards towards Gull Lake and lies at 85 m altitude. When unfrozen, the site is permanently flushed from a watershed at the base of a moraine ridge which separates the slope from the western end of Brown Mountain. Continual flushing has allowed the development of a soligenous, nutrient-rich bog, considerably less acid than the *Polytrichum* bog at Site 2. The substrate thus consists of a superficial layer of *Tortula* litter 10-12 cm thick (pH 5.6) overlying a narrow of saturated peat (pH 5.1), below which is fine glacial till (pH 6.2).

II. — METHODS

Material for the determination of testate rhizopod populations was sampled on 15 occasions at monthly intervals from November 1978 to February 1980. On each occasion, at each site, material was sampled from an upper horizon (0-3 cm) of litter of humus and from a lower horizon (3-6 cm) of underlying peat or soil. Material was sampled from five randomly located points within each site and combined to give a pooled sample for the site.

Snow cover at each site was monitored throughout the study period. Weekly screem temperature maxima and minima and grass minima were recorded at the meterological station near Site 1 (Fig. 2). Temperature readings by thermistor probes placed at + 0.5 cm, — 0.5 cm and — 5.0 cm on Site 3 were read at noon ± 2 hr at approximately 5-day intervals from December 1978 to December 1979. The moisture content of the materials sampled was measured during the latter part of the study period, July 1979 to February 1980.

Testate rhizopod species were enumerated by the direct observation technique of COÛTEAUX (1967), as used by SMITH (1973 b, 1978). 0.5 g sub-samples of fresh material were chopped to a fine mince, fixed in Bouin's solution and diluted by x 500. The dilute suspension was stirred for 2 hr and aliquots filtered through 0.45 grade Oxoid membrane filters. Sections of filter bearing 4 mg soil material were cleared in xylene and mounted in Canada balsam ; ten replicate slides were prepared for each sample. By this method, populations of testate rhizopods were determined as numbers of live individuals g^{-1} of soil fresh weight with 25 individuals g^{-1} as the threshold of detectability. Population estimates for the period July 1979 to February 1980 were converted to numbers cm^{-2} using a regression of soil moisture derived from previous measurements on 24 cores from Sites 1 and 2 (Fig. 3): Log $y = 0.19\text{-}0.13x$, where y = soil density g cm^{-3} dry weight and x = soil moisture fraction dry weight.

III. — RESULTS AND DISCUSSION

A — The physical environment.

The records of weekly screen maximum and minimum and grass minimum temperatures near Site 1 (Fig. 4) illustrate the oceanic nature of the

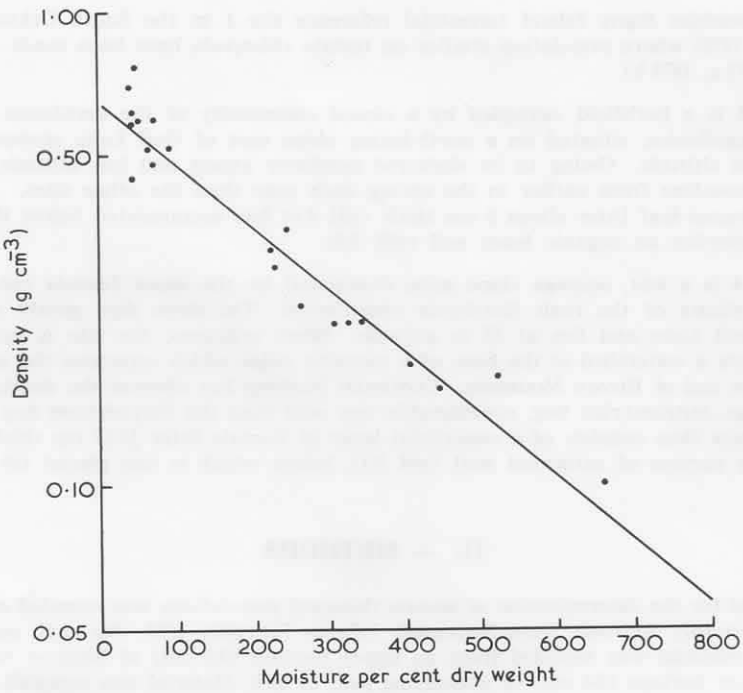
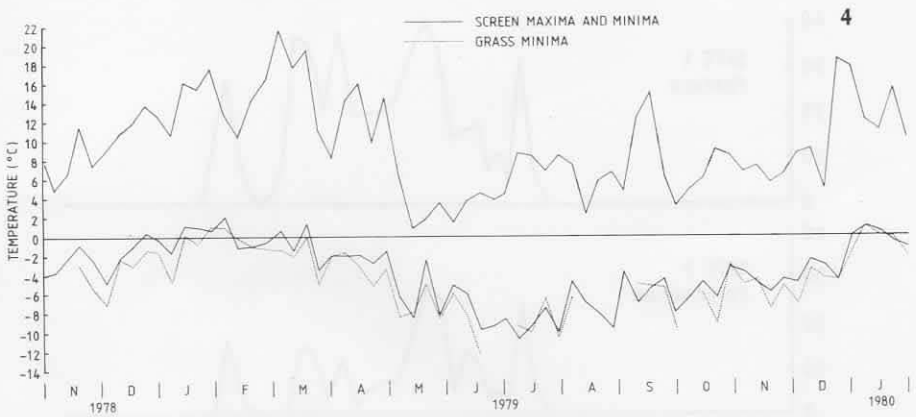


FIG. 3. — Regression of soil density on moisture content of cores taken from sites 1 and 2. Log y = 0.19 — 0.13 x.

temperature regime of coastal South Georgia. There was a small seasonal temperature range (— 12° to + 22° C), weekly screen maxima were above 0° C throughout the 1979 winter and both screen and grass minima were close to 0° C during the midsummer months, January and February.

Inspection of thermistor probe records from Site 3 (Fig. 5) together with the records of snow cover (Fig. 6) shows that temperatures close to the ground surface at noon ± 2 hr were very close to 0° C throughout the midwinter period of continuous snow cover (May through August 1979). The peaks of temperature above 0° C in mid-May, early June, the end of July and mid-September coincide with periods of reduced depth of snow cover at all four sites. These coincidences suggest that most of the week-to-week variation in snow cover was a function of the temperature prevailing in both the Maiviken and King Edward Cove areas, rather then of local snow drifting induced by wind. Thus the micrometeorological conditions which existed at Site 3 *(Acaena)* in winter may be taken to be broadly representative of those at Sites 1 and 2 *(Festuca* and *Polytrichum)* also, since they experienced similar patterns of snow cover in magnitude, duration and variation, even though they are more than 3 km distant. This contention is supported by the observation that fortnightly temperatures at + 0.5 cm recorded at Sites 1 and 2 throughout 1977 and 1978 (M. J. SMITH, 1982) show a remarkably similar pattern to the present data for Site 3 in 1979. However Site 4



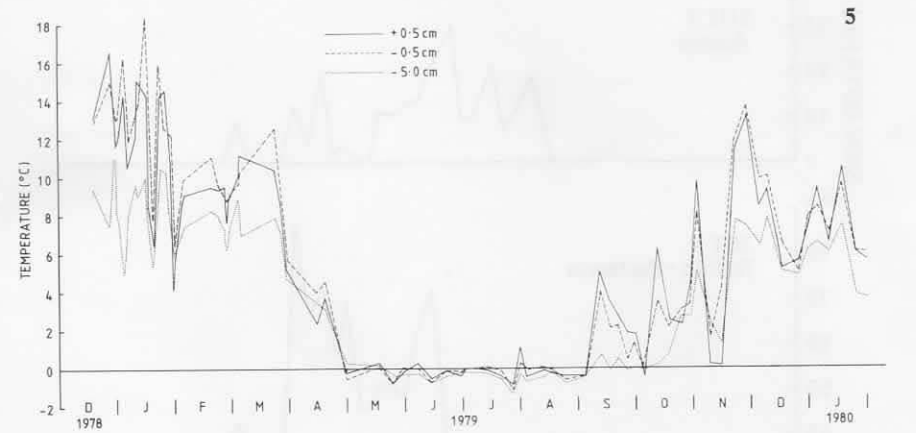


FIG. 4. — Weekly maximum and minimum Stevenson Screen temperatures and minimum grass temperatures at Maiviken Meteorological Station November 1978-January 1980. FIG. 5. — temperature readings at non ± 2 hour by thermistor probes at + 0.5 cm, — 0.5 cm and — 5.0 cm on site 3.

(Tortula-Rostkovia), influenced by the local topography, was snow-covered to a greater depth and for a period that extended later into the spring months, October and November, and may thus have been subjected to stable temperatures close to 0° C for a longer period.

During the spring and summer months (December 1978 - April 1979 and October 1979 - January 1980), the recorded noon ± 2 hr temperatures at Site 3 (Fig. 5) showed considerable short-term fluctuations, but were continuously above 0° C. However the weekly grass minima recorded near Site 1 were continuously below 0° C, except during January 1980; it is thus very probable that the sites were subject to significant diurnal fluctuations in temperature and changes of ± 12° C at the ground surface within 12 hr may have occurred frequently. Thus biota which could actively inhabit this stra-

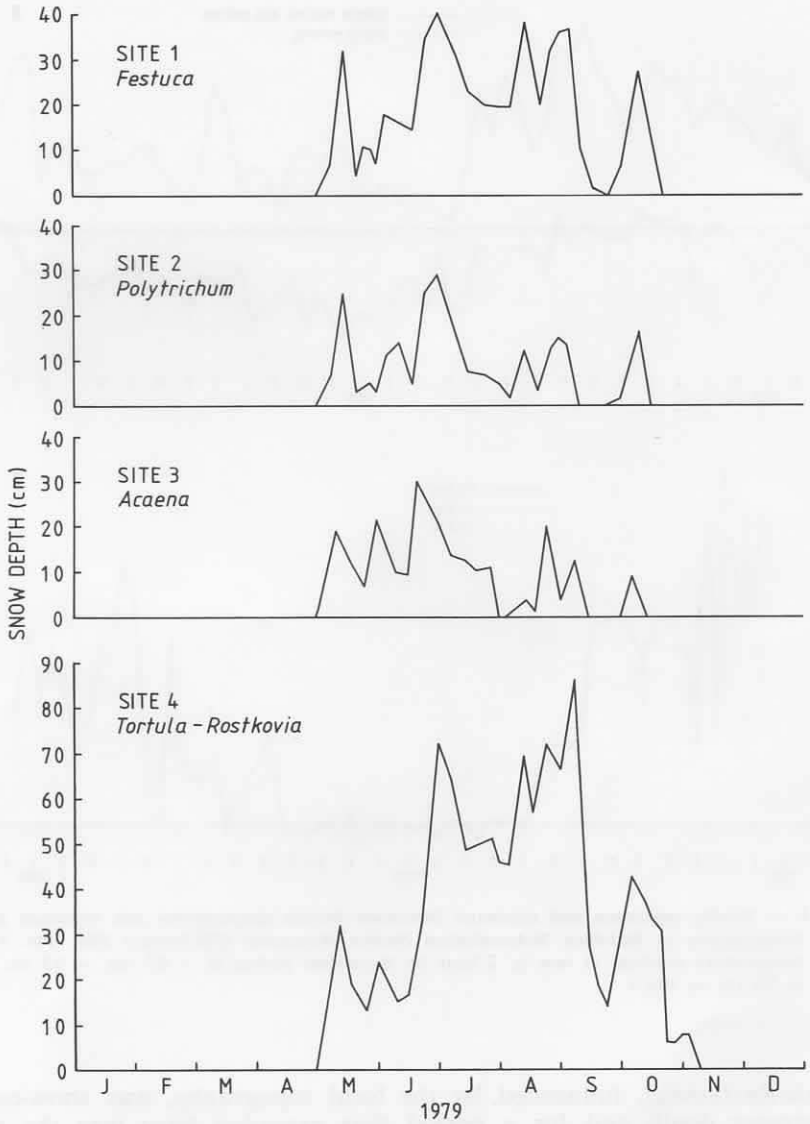


FIG. 6. — Mean depth of snow cover at the study sites.

tum and show growth under this temperature regime must be adapted to tolerate frequent fluctuations above and below 0° C, but not necessarily extreme sub-zero temperatures.

The moisture content of the cores, taken for estimation of testate rhizopod populations, is shown in Fig. 7. These results demonstrate the considerable build of ice within the soils and peats at all four sites in midwinter followed by a steep reduction in moisture content during the spring melt

period. As with the snow-cover data, Sites 1, 2 and 3 showed considerable mutual similarity, whilst the cores from Site 4 showed a higher moisture content later into the spring which remained greater than 400 % dry weight into midsummer. These observations can be clearly associated with the local topography and hydrology of Site 4, it being a mire flushed by water draining into Gull Lake.

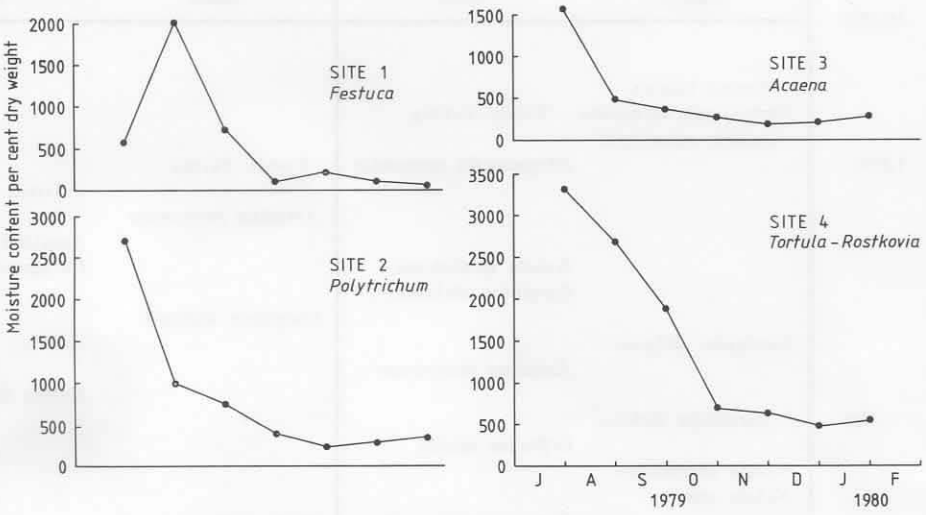


FIG. 7. — Moisture content of soil cores taken from the study sies July 1979-February 1980. (Same label axis for sites 1, 2 and 3 as for site 4).

B — **Abundance of the testate rhizopod fauna.**

18 species of testate rhizopod were recorded from the four sites with populations exceeding the threshold of detectability (25 individuals g^{-1} fresh weight) on at least one sampling occasion:

Arcella arenaria Greeff;
Centropyxis aculeata (Ehrenberg);
Centropyxis aerophila Deflandre;
Difflugia lanceolata Penard;
Difflugia longicollis Gassowsky;
Difflugia lucida Penard;
Difflugia penardi Wailes;
Nebela dentistoma Penard;
Nebela martiali Certes;
Nebela vas Certes;
Nebela wailesi Deflandre;
Phryganella acropodia (Hertwig and Lesser);
Trigonopyxis arcula (Leidy);
Assulina muscorum Greeff;

TAB.

Annual mean abundance of testate rhizopods

Numbers g^{-1} fresh weight	Site 1 : *Festuca*		Site 2 : *Polytrichum*	
	upper	lower	upper	lower
10,000				
	TOTAL FAUNA			
	Phryganella acropodia	TOTAL FAUNA		
	Assulina muscorum			
1,000	—	*Phryganella acropodia*	TOTAL FAUNA	
				TOTAL FAUNA
			Assulina muscorum	
				Assulina muscorum
		Nebela dentistoma		*Phryganella acropodia*
		Corythion dubium		
			Corythion dubium	
	Euglypha strigosa			
		Assulina muscorum		
				Nebela dentistoma
100	— *Corythion dubium*			
		Difflugia lucida		
	Nebela dentistoma			
	Nebela vas			
		Trigonopyxis arcula	*Phryganella acropodia*	
				Corythion dubium
	Difflugia lucida		*Euglypha strigosa*	
		Nebela vas		
	Trigonopyxis arcula		*Difflugia lucida*	
	Nebela martiali		*Centropyxis aerophila*	*Trigonopyxis arcula*
		Corythion dubium		
10	—			*Nebela vas*
				Euglypha strigosa
			Centropyxis aculeata	
	Centropyxis aculeata			*Nebela martiali*
		Centropyxis aculeata		
	Difflugia penardi			
			Trigonopyxis arcula	*Difflugia lucida*
	Arcella arenaria			

Corythion dubium Taranek;
Euglypha rotunda Wailes and Penard;
Euglypha strigosa (Ehrenberg);
Trinema enchelys (Ehrenberg).

The mean annual abundance of these species in the upper and lower horizons of each of the four sites is shown in Table I. *Phryganella acropodia* was in general the most ubiquitous abundant species. It shared

I

in terrestrial habitats on South Georgia 1978-1980

Site 3 : *Acaena*		Site 4 : *Tortula-Rostkovia*	
upper	lower	upper	lower
			TOTAL FAUNA
			Phryganella acropodia
	TOTAL FAUNA		
	Phryganella acropodia		
			Centropyxis aculeata
TOTAL FAUNA			
		TOTAL FAUNA	
Phryganella acropodia			
Centropyxis aerophila			*Centropyxis aerophila*
	Centropyxis aerophila	*Centropyxis aculeata*	
		Phryganella acropodia	
			Arcella arenaria
		Centropyxis aerophila	
	Difflugia lucida		
	Trigonopyxis arcula	*Nebela wailesi*	
			Difflugia lucida
		Arcella arenaria	
			Nebela wailesi
Nebela dentistoma			
Arcella arenaria			
Difflugia lucida			*Corythion dubium*
	Arcella arenaria	*Corythion dubium*	
Trigonopyxis arcula	*Nebela dentistoma*	*Assulina muscorum*	
	Corythion dubium	*Difflugia lanceolata*	
Nebela wailesi			*Assulina muscorum*
	Assulina muscorum	*Difflugia lucida*	
Euglypha strigosa		*Euglypha rotunda*	
Corythion dubium	*Centropyxis aculeata*		
Trinema enchelys		*Nebela dentistoma*	
Difflugia longicollis		*Euglypha strigosa*	*Difflugia longicollis*
	Nebela wailesi		
Centropyxis aculeata		*Trinema enchelys*	
Assulina muscorum	*Euglypha strigosa*		

dominance of the fauna with *Assulina muscorum* and *Corythion dubium* in the Maiviken sites *(Festuca* and *Polytrichum)* and with *Centropyxis aculeata* and *Centropyxis aerophila* in the sites near Gull Lake *(Acaena* and *Tortula-Rostkovia).* Interestingly, *P. acropodia* has been recorded as the most abundant and frequent testate species in the European oak-beech and spruce forest soils investigated by COÛTEAUX (1975, 1976). However the other abundant species in those habitats were *Euglyphidion enigmaticum* and *Trinema complanatum,* species which have not been recorded at all in the sub-Antarctic.

The composition of the testate fauna of the *Polytrichum* moss-turf at Site 2 closely resembled that of *Polytrichum-Chorisodontium* moss-turf peat on Signy Island, South Orkney Islands (HEAL, 1965; SMITH, 1973 a, 1973 b), though single species dominance by *Corythion dubium* observed there was not evident on South Georgia. These data of faunal abundance for South Georgia are also broadly comparable to those for other sub-Antarctic islands: GROSPIETSCH (1971) recorded *Assulina muscorum, Corythion dubium* and *Nebela vas* as abundant on Marion Island and BONNET (1981) observed the testate fauna of Iles Kerguelen to be dominated by *Centropyxis aerophila.* By contrast, LAMINGER (1978) found that the testate fauna of high alpine meadow in Austria was dominated by *Trinema* spp., which occurred only rarely in South Georgia habitats.

The upper (0 — 3 cm) and lower (3 — 6 cm) horizons within each of the South Georgia sites had a similar species composition of testate rhizopod fauna, despite the two having different physical properties for all sites, except Site 2 *(Polytrichum),* and none of the species showed a consistent pattern in vertical distribution of abundance. Where the two horizons had different pH values, it was the more acid horizon which contained the greater abundance of testate rhizopods. However there was no simple association of pH with abundance between sites. These results for testate rhizopods are in contrast with observations on the microflora by M. J. SMITH (1982 and personal communication) who detected negative associations of log bacterial and log fungal numbers with depth and positive associations of them with pH in Sites 1 and 2 during 1977 and 1978.

Comparing the results for Site 4 (*Tortula-Rostkovia* bog) with those for the other three more acid sites reveals differences which show a similar pattern to the differences in frequency of occurence of testate species in various *Sphagnum* bogs and fens in England, recorded by HEAL (1961, 1964). His classification of *P. acropodia, C. dubium, A. muscorum* and *C. aculeata* as eurytope species of both fens and bogs, *Trigonopyxis arcula* as bog-specific, and *Trinema enchelys* as fen-specific, is consistent with present results. However his classification of *C. aerophila* and *Nebela dentistoma* as fen-specific species is inconsistent with present observations of their abundance in Sites 1, 2 and 3.

C — **Seasonal fluctuations in testate rhizopod populations.**

Month-to-month fluctuations in the estimated populations of the most abundant testate rhizopod species, expressed as numbers g^{-1} fresh weight, are shown in Figs 8, 9, 10 and 11. In this form the data do not show any definite pattern of seasonality and there is no consistency between sites, between horizons or between species. In several cases peak numbers seem to occur in winter when ground temperatures beneath the snow were close to 0° C. These data are in marked contrast to comparable observations on *Corythion dubium,* inhabiting *Polytrichum-Chorisodontium* moss-turf peat on Signy Island, South Orkney Islands, where a distinct pattern of winter low and summer high populations, clearly related to the seasonal temperatures, has been observed (SMITH, 1973 b). It may thus be inferred that an important factor in the absence of such a pattern on South Georgia was

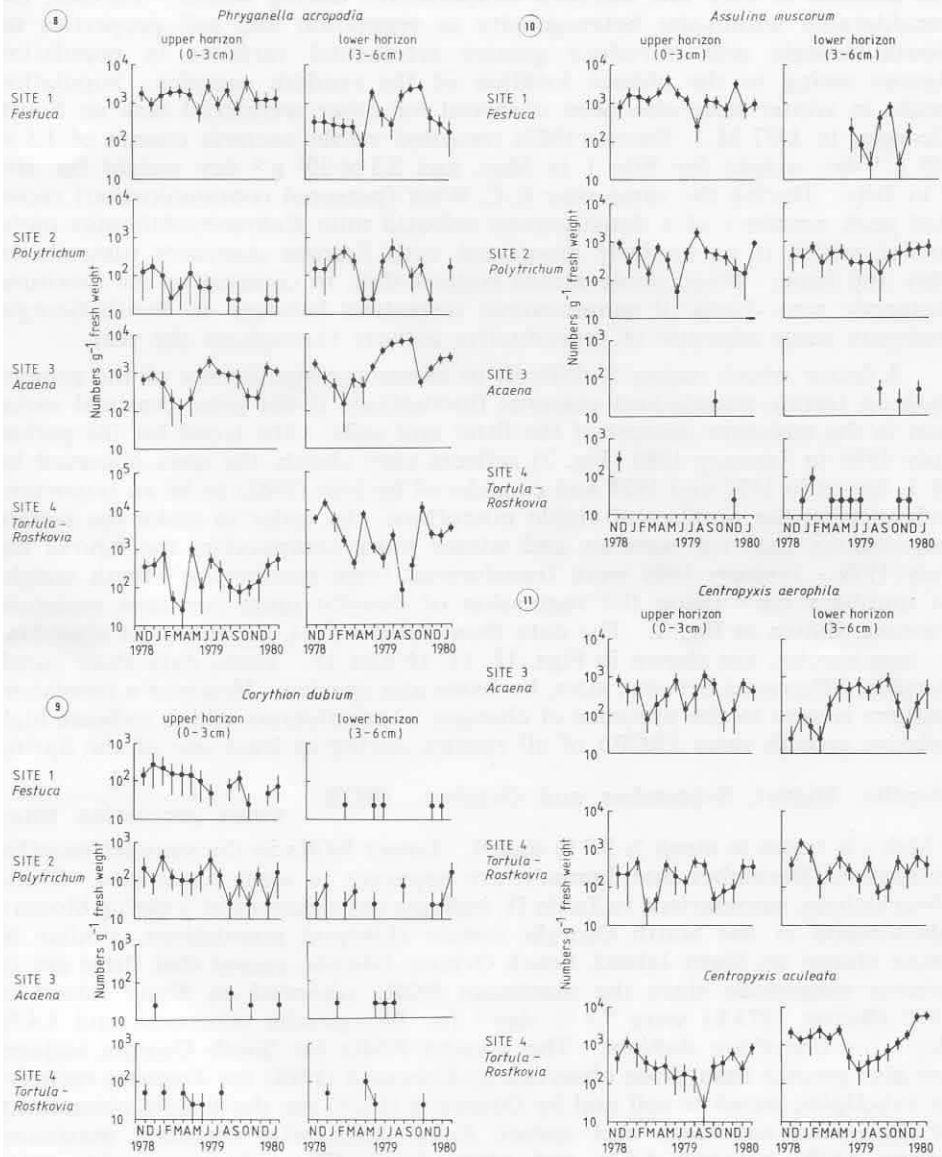
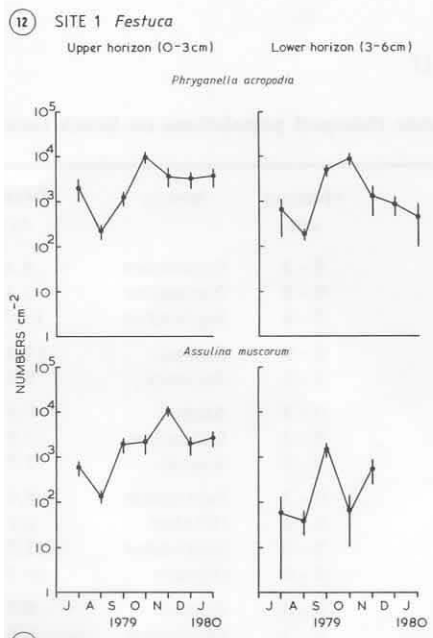


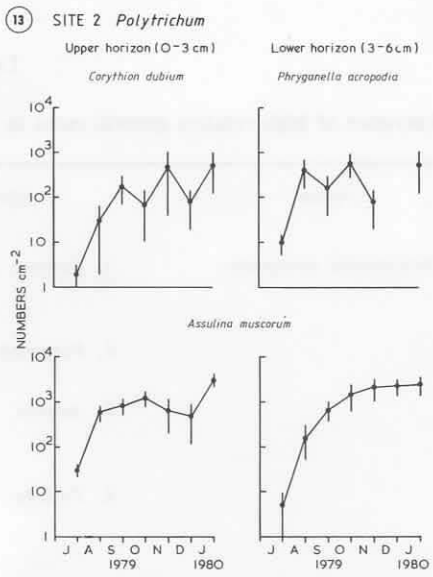
FIG. 8. — Live numbers of *Phryganella acropodia* in two horizons of the study sites. Figures plotted are means of the replicate estimates with standard errors. FIG. 9. — Live numbers of *Corythion dubium* in two horizons of the study sites. Figures plotted are means of ten replicate estimates with standard errors. FIG. 10. — Live numbers of *Assulina muscorum* in two horizons of the study sites. Figures plotted are means of ten replicate estimates with standard errors. FIG. 11. — Live numbers of *Centropyxis aerophila* and *Centropyxis aculeata* in two horizons of sites 3 and 4. Figures plotted are means of ten replicate estimates with standard errors.

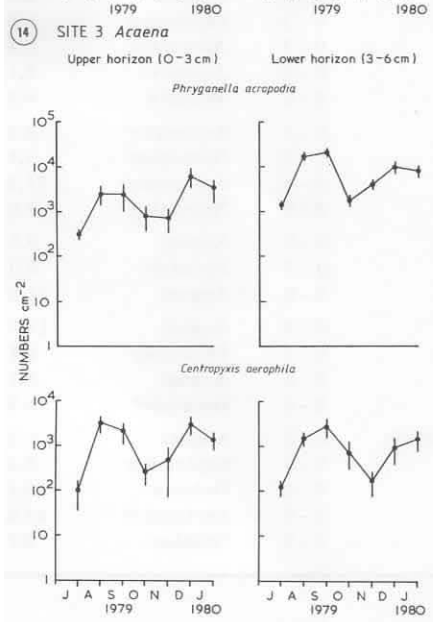
the absence of very low sub-zero temperatures during winter. Further, the considerable within-site heterogeneity in vegetation and soil properties on South Georgia will introduce greater artefactual variance in population figures owing to the chance location of the random samples. Population peaks in winter have also been observed for other terrestrial taxa on South Georgia: in 1977 M. J. SMITH (1982) recorded viable bacteria counts of 1.3×10^8 g^{-1} dry weight for Site 1 in May, and 2.5×10^8 g^{-1} dry weight for site 2 in July. During the same year C. C. WEST (personal communication) recorded peak numbers of a detritivorous oribatid mite *Eobrachychthonius oudemansi*, which is particularly associated with *Festuca contracta* tussocks, in May and June. These observations suggest that, in contrast to the maritime Antarctic zone, biota of snow-covered terrestrial habitats on South Georgia maintain some measure of reproductive activity throughout the year.

A factor which makes it difficult to assess the significance of the present data on testate populations seasonal fluctuations is the great seasonal variation in the moisture content of the litter and soils. The trend for the period July 1979 to January 1980 (Fig. 7) reflects very closely the ones observed by M. J. SMITH in 1977 and 1978 and considered by him (1982) to be an important influence on the number of viable microflora. In order to make the testate populations data for summer and winter more comparable, the figures for July 1979 - January 1980 were transformed from numbers g^{-1} fresh weight to numbers cm^{-2} using the regression of density upon per cent moisture content, shown in Fig. 3. The data thus transformed, for the most abundant testate species, are shown in Figs. 12, 13, 14 and 15. These data show considerable differences between sites, horizons and species. However a consistent pattern is seen in the presence of changes in populations which indicate high relative growth rates (RGR) of all species during at least one of the Spring months, August, September and October. ($RGR = \frac{1n2}{\text{mean generation time}}$; « high » is taken to mean $\geqslant 5.0$ % day^{-1}). Lower RGRs in the summer months, November, December and January, are apparent in some cases also. These observations, summarised in Table II, indicate the existence of « spring bloom » phenomena in the South Georgia testate rhizopod populations, similar to those shown on Signy Island, South Orkney Islands, except that these are of greater magnitude since the maximum RGRs recorded on Signy Island in 1970 (SMITH, 1973 b) were 7.4 % day^{-1} for *Phyrganella acropodia* and 4.4 % day^{-1} for *Corythion dubium*. The present RGRs for South Georgia testates are also greater than those observed by LAMINGER (1978) for *Trimena enchelys* in sub-Alpine meadow soil and by COÛTEAUX (1975) for the testate community of European oak-beech and spruce forest soils, who recorded maximum spring RGRs between 3.5 % and 6.9 % day^{-1}. The only comparable rates observed are those for testates inhabiting montane aspen woodland soil in Canada, where a RGR of 11.4 % day^{-1} was recorded for the testate population of the humus layer of plots in which the moisture content had been artificially increased (LOUSIER, 1974).

It seems likely that the periods of high RGR among the testate rhizopod populations are consequent upon bursts of population growth activity by the microflora. M. J. SMITH's (1982) observations on numbers of viable bacteria and viable fungal propagules in 1977 and 1978 indicate the existence of RGRs







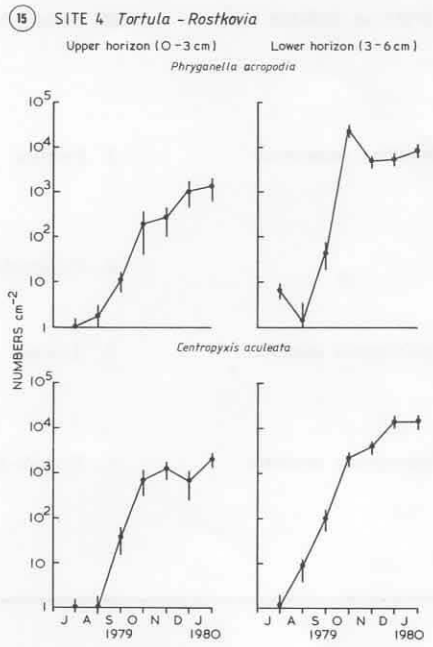


FIG. 12. — Live numbers cm^{-2} of the abundant species in two horizons of Site 1. Figures plotted are means of ten replicate estimates with standard errors. FIG. 13. — Live numbers cm^{-2} of the abundant species in two horizons of Site 2. Figures plotted are means of ten replicate estimates with standard errors. FIG. 14. — Live numbers cm^{-2} of the abundant species in two horizons of Site 3. Figures plotted are means of then replicate estimates with standard errors. FIG. 15. — Live numbers cm^{-2} of the abundant species in two horizons on Site 4. Figures plotted are means of ten replicate estimates with standard errors.

TAB. II

Occurrence of high relative growth rates in testate rhizopod populations on South Georgia

Species	Site	Horizon cm	Month	RGR % day^{-1}
Phryganella acropodia	1. *Festuca*	0 - 3	September	8.4
		0 - 3	November	5.4
		3 - 6	September	10.2
	2. *Polytrichum*	3 - 6	August	12.4
		3 - 6	January	6.6
	3. *Acaena*	0 - 3	August	6.8
		0 - 3	December	7.0
		3 - 6	August	7.7
	4. *Tortula*	0 - 3	September	6.0
		0 - 3	October	9.7
		3 - 6	September	11.7
		3 - 6	October	20.7
Corythion dubium	2. *Polytrichum*	0 - 3	August	8.7
		0 - 3	September	5.8
		0 - 3	November	6.4
		0 - 3	January	6.1
		3 - 6	January	6.3
Assulina muscorum	1. *Festuca*	0 - 3	September	8.4
		0 - 3	November	5.4
		3 - 6	September	11.4
		3 - 6	November	7.0
	2. *Polytrichum*	0 - 3	August	9.5
		0 - 3	January	6.0
		3 - 6	August	11.5
Centropyxis constricta	3. *Acaena*	0 - 3	August	11.0
		0 - 3	December	6.1
		3 - 6	August	8.1
		3 - 6	December	5.9
Centropyxis aculeata	4. *Tortula-Rostkovia*	0 - 3	August	6.3
		0 - 3	September	8.4
		0 - 3	October	10.1
		3 - 6	September	14.6
		3 - 6	October	9.7

between 4.9 and 10.0 % day^{-1} for these taxa on both Site 1 and 2. Since these are different years from the one of present observations, the exact temporal relationship between microfloral and microfaunal blooms on South Georgia cannot be established. However the evidence is generally consistent with their being causally related and initiated by the release of soil nutrients coincident with the spring melt in a manner similar to that proposed for

moss-turf peat biota on Signy Island, in the maritime Antarctic, by WYNN-WILLIAMS (1980).

The appearance of high RGRs as early as August 1979 is difficult to explain since ground surface and soil temperatures were $\leqslant 0^{o}$ C throughout August, apart from a short-lived thaw at the beginning of the month (Fig. 5). It is possible that localised zones within the sites, not detected by the thermistor probes in Site 3, experienced above zero temperatures and became flushed with nutrients underneath the snow before the general melt in September and thus initiated early bursts of population activity.

The months in which high RGRs occurred were usually the same for the two horizons within each site. This observation can be related to the uniformity of winter temperatures recorded for the depths — 0.5 cm and — 5.0 cm (Fig. 5), so that the initiation of population growth occured synchronously in the two horizons. The temporal separation of Spring blooms with depth, that was observed in Signy Island moss-turf peat (SMITH, 1973 b), as the melt progressed from the surface to the lower horizons, was not apparent on South Georgia.

The three most abundant species in Sites 1 and 2, *P. acropodia, C. dubium* and *A. muscorum* (Figs. 12 and 13) showed more or less simultaneous population blooms within each site and horizon early in the spring (August and September) but later in the summer their population peaks became asynchronous suggesting the possibility of exhaustion of essential resources and the development of allelopathic relations between the species. In Sites 3 and 4, however, the *Centropyxis* spp. showed almost exact synchrony with *P. acropodia* throughout the spring and summer (Figs 14 and 15) suggesting that the species within each site were being similalry influenced by the environment. The results for Site 4 *(Tortula-Rostkovia)* are particularly remarkable, not only because the RGRs are extremely high, but also because they were maintained through consecutive months. It seems likely that these phenomena were associated with Site 4 being a soligenous mire continuously flushed with nutrients throughout the spring and maintaining a high moisture content (Fig. 7). Thus conditions supporting continuous population growth at an exceptionally high rate were sustained at this site, compared with the short-term bursts of growth evident at the other sites. It has been recently reported (COÛTEAUX and PUSSARD, 1983) that *Phryganella acropodia* can utilise fungal filaments and propagules as food but that *Centropyxis aerophila,* does not grow at the expense of the fungi that readily sustain *P. acropodia.* Most testates are thought to utilise bacteria and algae only (LAYBOURN and WHYMANT, 1980) and it seems likely that *Assulina muscomum* and *Corythion dubium* are also non-fungal feeders (COWLING and SMITH, 1982). It is possible that the patterns of testate population fluctuations on South Georgia were in part a result of *P. acropodia* being the only abundant species able to exploit fungi as food. Thus *P. acropodia* showed co-dominance with the bacterial feeders in the early spring when resources were non-limiting, whilst the asynchronous population peaks of the summer might reflect asynchronous peaks of bacterial and fungal food availability, especially in Sites 1 and 2 where stress due to low moisture content occurred.

The magnitudes of the RGRs observed at all the sites, but especially at

Site 4 (Tab. II), are surprising in that they equal or exceed the RGRs determined from laboratory cultures or testate rhizopods, at temperatures comparable to those recorded in the field. In a pilot experiment SMITH (1973 c) noted RGRs of 11.3 % day^{-1} at 18° C and 15.6 % day^{-1} at 25° C for a *Euglypha rotunda* strain of temperate provenance. Using *Corythion dubium* and *Euglypha rotunda* strains of maritime Antarctic provenance, and also greatly improved culture conditions, COWLING (1983 and personal communication) has recently recorded RGRs of 2.2 — 6.2 % day^{-1} at 5° C, 5.3 — 15.1 % day^{-1} at 10° C and 15.3 — 27.1 % day^{-1} at 20° C. MEISTERFELD (1981) has recorded RGRs for several *Arcella* and *Centropyxis* species with maxima between 12.0 % and 135.2 % day^{-1} at 25 — 30° C, including a value of 65.5 % day^{-1} for *Centropyxis aculeata*. Since the maximum recorded field temperature on South Georgia at grass level during spring 1979 was 13.5° C (Fig. 4), the RGRs observed in the field (Tab. II) are remarkably high, even if some temperature maxima higher than 13.5° C occurred but were not recorded. These results lend weight to the hypothesis already advanced (SMITH, 1973 c, 1982 a) that the adaptation shown by the species of testate rhizopods, that are abundant in the sub-Antarctic and maritime Antarctic, to their ambient temperature regime, is not an exceptional ability to sustain high growth rates at low temperatures, but rather a capacity to « switch on » rapidly and exploit successfully the periods during which temperatures above ca. 10° C prevail. Such periods may be frequent, but their continuous duration is never more than a few hours.

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SUMMARY

The populations of 18 species of testate rhizopod, at four sites with contrasting vegetation and soil types on the sub-Antarctic island of South Georgia, were determined at monthly intervals from November 1978 to January 1980. The abundant species at the sites with the more acid soils and peats, (pH 3.9 — 4.2) were *Phryganella acropodia, Assulina muscorum* and *Corythion dubium*. The fauna of the less acid soils (pH 4.6 — 5.6) were dominated by *Centropyxis aerophila* and *Centropyxis aculeata* as well as *P. acropodia*. The largest populations were present in a flushed soligenous mire dominated by *Tortula* moss and *Rostkovia* rushes. Similarities to the testate fauna of soils and peats on maritime Antarctic and other sub-Antarctic islands were evident and limited comparisons to those of *Sphagnum* bog, Alpine meadow and Lowland woodland soils in the northern hemisphere could also be drawn. Fluctuations in the testate populations did not show any consistent seasonality, but all the abundant species underwent populations blooms during the spring months, when relative growth rates exceeding 5.0 % day^{-1} were evident.

RÉSUMÉ

Écologie des populations de Thecamoebiens terricoles de l'île sub-antarctique de South Georgia

Le recensement mensuel, de novembre 1978 à janvier 1980 de 18 espèces de Thécamoebiens a été réalisé dans quatre stations très différentes du point de vue du type de végétation et des types de sol. *Phryganella acropodia*, *Assulina muscorum* et *Corythion dubium* sont les espèces les plus abondantes dans les stations de sols et de tourbes les plus acides (pH 3.9-4.2). La faune des sols moins acides (pH 4.6-5.6) est dominée par *Centropyxis aerophila* et *Centropyxis aculeata* et également par *Phryganella acropodia*. Les populations les plus abondantes ont été trouvées dans une fange terreuse inondée dominés par une mousse du genre *Tortula* et un jonc du genre *Rostkovia*. Les ressemblances avec la faune thécamoebienne des sols et des tourbes de quelques autres îles subantarctiques sont évidentes, des comparaisons ont été faites avec la faune des sphaignes, des prairies alpines et des sols forestiers de l'hémisphère nord. Les variations mensuelles des effectifs ne montrent pas de périodicité, cependant toutes les espèces voient leur densité croître au printemps, pendant lequel le taux de croissance relative est plus grand que 5,0 % jour^{-1}.

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